Use of tri-axial accelerometers to assess terrestrial mammal behaviour in the wild

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Running title

AcTags used to assess terrestrial mammal behaviour

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Abstract

Tri-axial accelerometer tags provide quantitative data on body movement that can be used to characterise behaviour and understand species ecology in ways that would otherwise be impossible. Using tags on wild terrestrial mammals, especially smaller species, in natural settings has been limited. Poor battery power also reduced the amount of data collected, which limits what can be derived about animal behaviour. Another challenge using wild animals, is acquiring observations of actual behaviours with which to compare tag data and create an adequate training set to reliably identify behavioural states.

Brown hares were fitted with accelerometers for five weeks to evaluate their use in collecting detailed behaviour data and activity levels. Collared hares were filmed to associate actual behaviours with tag data. Observed behaviours were classified using Random Forests (ensemble learning method) to create a supervised model and then used to classify hare behaviour from the tags.

Increased tag longevity allowed acquisition of large quantities of data from each individual and direct observation of tagged hare's behaviour. Random Forests accurately classified observed behaviours from tag data with an 11 % error rate. Individual accuracy of behaviours varied with running (100 % accuracy), feeding (94.7 %) and vigilance (98.3 %) having the highest classification accuracy. Hares spent 46 % of their time being vigilant and 25 % feeding when active.

The combination of our tags and Random Forests facilitated large amounts of behavioural data to be collected on animals where observational studies could be limited, or impossible. The same method could be used on a range of terrestrial mammals to create models to investigate behaviour from tag data, to learn more about their behaviour and be used to answer many ecological questions. However, further

development of methods for analysing tag data is needed to make the process quicker, simpler and more accurate.

Key-words: 3DA, *Lepus europaeus*, activity, behaviour, random forests, classification, brown hare

Introduction

Understanding animal behaviour typically requires hours of direct observation of individuals in the wild, which is particularly difficult when species are elusive or hard to view. 'Biologging' technology, where activity is remotely monitored by accelerometer tags attached to the study animal, has been successfully used to study marine animal behaviour (Wilson *et al.*, 1996; Yoda *et al.*, 1999; Bograd *et al.*, 2010; Gallon *et al.*, 2012), but its use on wild terrestrial species has been more limited (Wilson *et al*., 2008). The availability of mass-produced movement sensors for mobile phones has enabled the development of relatively low cost solutions that allow continuous data collection (Rai *et al.*, 2012). Early studies used only one or two sensors attached to the animal (Yoda *et al.*, 2001; Sakamoto *et al.*, 2009), but now three sensors (tri-axial accelerometers) can collect acceleration data along three axes of movement; X, Y and Z, (heave, surge and sway), as well as recording a time stamp (Gjoreski, Gams & Chorbev, 2010), which provides greater detail of temporal patterns in body movement (Bograd *et al.*, 2010).

Tri-axial accelerometer tags (3DA-Tags) provide quantitative data on body movement which can be used to characterise and quantify behaviour. This data can be used to understand species ecology by linking animal behaviour, movement and activity levels with data on habitat use in ways which would otherwise be impossible (Shepard *et al.*, 2008; Gao *et al.*, 2013). A number of machine learning methods have been employed such as linear discriminant analysis, Random Forests and artificial neural networks (Ravi *et al.*, 2005; Gjoreski *et al.*, 2010; Fortmann-Roe *et al.*, 2011; Gao *et al.*, 2013) but there is a lack of standard practice in these analyses. A user friendly standardised method that can be repeated between studies of the same or similar species still requires further development (Campbell *et al.*, 2013; Gao *et al.*, 2013).

Many studies of terrestrial species' activity have been conducted on larger mammals such as humans (Ravi *et al.*, 2005; Gjoreski *et al.*, 2010; Gao *et al.*, 2013), or captive and tame animals such as, dogs (*Canis lupus familiaris*), badgers (*Meles meles*) and domestic cats (*Felis catus*) (Campbell *et al.*, 2013; Gao *et al.*, 2013; Watanabe *et al.*, 2005). The use of 3DA-Tags on wild mammals, especially on smaller species in natural settings has been limited. A major challenge in using wild animals is acquiring observations of actual behaviours of tagged animals with which to correlate tag data (Gao *et al.*, 2013).

We used the 'AcTag' a 3DA based tag similar to one previously used on badgers (Noonan *et al.*, 2014), to quantify brown hare activity by correlating direct observations with recorded accelerometry data. There has been limited direct behavioural observation studies on brown hares in the wild but they were restricted to studying hares in short vegetation at dawn or dusk (Marboutin and Aebischer 1996), or using a feeding station rather than natural settings (Monaghan and Metcalfe 1985). Many studies of hare behaviour have used radio tracking to quantify space use (Tapper & Barnes, 1986; Stott, 2003) and make comparisons between day and night, resting and feeding activity levels (Marboutin & Aebischer, 1996; Petrovan, Ward & Wheeler, 2013). Our use of AcTags to collect behavioural data on hares provided a novel opportunity to collect large quantities of behavioural data from each individual hare, particularly at times when visibility was poor due to tall vegetation, or light levels, and gave a detailed insight into their daily activity that was previously not possible. Using this new type of 3DA based tag (AcTag) made it possible to record all three axes of movement for an unprecedented amount of time for 3DA recordings on an animal of this size.

In this paper we present the first field-scale study of accelerometer-derived behaviour of a medium-sized terrestrial species based entirely on wild individuals. Our work combines field observation with characterisation of individual behaviours and classification of accelerometer data to report novel observations on the behaviour of a species of conservation concern from full 24 hour monitoring using the tags.

Materials and methods

Capturing and tagging hares

The study site was located in Wykeham, North Yorkshire, UK, (54°12’59.21” N, -0°30’54.05” E) a landscape of lowland mixed arable and pastural farmland.

Five adult hares were captured and AcTags (Biotrack Ltd., Dorset, UK) were attached using collars fixed around the neck of four female hares and one male in August 2012 over 2 days. At least 5 people flushed hares into three 6z gauge static nylon long nets (Euroguns, Yorkshire, UK) (Petrovan *et al.*, 2013). To reduce stress each hare was handled and released within 10 minutes of capture. AcTags weighed less than 1 % of the hare’s body weight and were fitted using a TW-3 medium mammal cable tie (Biotrack Ltd., Dorset. UK). AcTags integrated a tri-axial accelerometer sensor (3DA), each axis sampling at 16Hz; a 2.4 GHz Zigbee compliant Wi-Fi radio transceiver, capable of transmitting data to a handheld directional antenna and associated base-station, and a microprocessor that stored data losslessly onto 2 GB SD memory card (for full details of the AcTag specification and system see Markham *et al.* (2012)). The AcTags also had a 173 MHz VHF tracking transmitter to allow location of animals using conventional radio tracking equipment. The capturing and tagging of hares were carried out in accordance with the University of Hull’s Ethical Committee protocols.

Tracking and remote downloading

VHF radio tracking (Telonics TR-4 radio receiver (Telonics Inc, Arizona, USA) and handheld Lintec flexible 3-element Yagi antenna (Biotrack Ltd., Dorset. UK)) was used to locate the tagged hares on a daily basis, and the Wi-Fi antenna was used to download

stored data from the AcTags remotely onto the base station once within about 200 m range.

Data were collected for up to 5 weeks, although one female hare died 2 weeks after tagging and one collar failed to record any data. Therefore, the analysis was carried out using data from the remaining four hares (Table 2). Data downloaded from the base station were unpacked into a MySQL database and exported as a CSV file.

Filming behaviours of tagged hares

Tagged hares were located and filmed in order to characterise behaviours. Hares were filmed over eight evenings using a Sony Handycam Hybrid HDD DCR – SR35 with a 40x optical zoom. Hares were identified before filming by homing in with the VHF and Wi-Fi antennae followed by visual confirmation of the tracking collar.

Once identified a hare was filmed continuously until either it moved out of sight, or the light levels were too low (as per Monaghan & Metcalfe, 1985). Recordings were made of four hares to collect examples of different hare behaviours, totalling 160 minutes of footage (mean per hare = 53.33 minutes, SD = 20.82 minutes). Individual periods of behaviours were logged with start and finish times in order to align them with output from AcTags.

Data analysis

Classification of known behaviours

The 3DA data were synchronised with the filmed behaviours using clear behavioural transitions (e.g. from resting to moving) to precisely align video footage with the AcTag timestamp. The 3DA data were then coded with a behaviour type (Table 1). Nine behaviours were identified from the video footage of the hares and 'matched' with the corresponding 3DA data recorded for those hares (Fig. 1): 1 = Resting; 2 = Running; 3 = Vigilance; 4 = Feeding; 5 = Scratching; 6 = Licking; 7 = Shaking; 8 = Hopping; 9 = Stretching

A total of 573 'bouts' of behaviour were used to create a classification model for these behaviours. For each bout of known behaviour a series of summary statistics were calculated (mean, standard deviation, minimum, maximum, kurtosis and skewness for each axis respectively, Table 2) and used to train a Random Forest model (an ensemble learning method for classification) (Breiman & Cutler, 2001; Lush *et al*., 2015). The use of classification trees has been found to be the most accurate for classifying behaviours from accelerometer data, with accuracy results of 84 % using decision trees (Ravi *et al.*, 2005) and 85 % using Random Forests (Gjoreski *et al.*, 2010; Fortmann-Roe *et al.*, 2011).

R (version 3.0.1, R Core Team 2013) was used to run the Random Forest model using the 'randomForest' package (Liaw & Wiener, 2002) and the graphical user interface, RATTLE (R Analytical Tool To Learn Easily, Williams 2011). The model was created by randomly selecting 75 % of the data and validated using the remaining 25 %

(Fielding, 2007). The behaviour code was set as the target variable, 500 trees were 'grown' with 4 variables at each split at the node of the trees; the model is not usually sensitive to changes to these variables (Liaw & Wiener, 2002). An importance graph was also produced to see which variables were the most important in classifying behaviours (Fig. 2).

Supervised Classification using Random Forest

The full 3DA datasets for all four hares were split into 5 second windows using R (Rai *et al.* 2012). Summary statistics were calculated for each 5 second window for each hare using R and the package "plyr" (Wickham, 2011). Condensing the data into windows and converting the raw data into a set of behaviours has been found to be more robust and have greater classification accuracy than using the raw data (Gjoreski *et al.*, 2010; Rai *et al.*, 2012).

A total of 18 attributes were calculated per 5 second window of the three axes (X, Y, Z) (Nathan *et al.*, 2012). The summarised dataset was then run through the Random Forest model created using known behaviours, and a behaviour class was allocated to each 5 second window by supervised classification using Random Forests.

Data were then coded by time of day i.e. dawn, day, dusk and night, to capture changes in daylight hours and to assess if behaviour changed at different times of the day. Sunrise and sunset times for that period were used with an hour either side to denote dawn or dusk (Petrovan *et al.*, 2013). To account for the difference in amount of overall time between the times of day, (i.e. day time = 10 hours compared to dawn which was

214 only 2 hours long), the mean proportion of time was calculated for each behaviour and
215 time of day. Proportion data were logit transformed to meet the assumptions of
216 homogeneity and normality. An ANOVA was performed in SPSS (IBM version 19) to
217 test if there were any differences in behaviours at different times of day and to calculate
218 average activity levels during the day. For the ANOVA analysis, resting and crouching
219 were combined to create the variable "resting" and licking, scratching and shaking were
220 combined to create a new variable called "grooming". To assess active and non-active
221 periods the variables resting, vigilance and crouching were combined to denote
222 'inactive' and running, feeding, licking, shaking and scratching were combined to
223 denote 'active'.

224

225 The number of daylight hours reduced from 14.34 hours to 12.17 hours over the course
226 of the AcTag data collection. To assess if this had an effect on hare behaviour the data
227 were split into periods of 12.5 – 13.5 daylight hours and 13.5 – 14.5 daylight hours. A
228 two-way ANOVA was performed to test if the amount of daylight hours affected
229 behaviour at different times of the day.

Results

Nearly 500 million 3DA data points were recorded from all tagged hares (Table 3).

Classification of behaviours

The Random Forest model created using the training data had an error rate of 10.47 %. The model classified running, feeding and vigilance behaviours well, but this was not the case for licking, hopping and stretching (Table 4). The other behaviours of resting, scratching and shaking were moderately well classified. The variable importance graph showed that the mean, standard deviation, minimum and maximum, in particular of the Z and Y axis, were more important in the classification of behaviours than other components of parameter estimates (Fig. 2).

Model validation of the test data used on the trained model, correctly classified (true positives) in 89 % of cases with the remaining 11 % incorrectly classified (false positives).

Daily activity and behaviours

The mean proportion of time hares spent running, feeding and grooming was significantly different between different times of the day (Table 5). However, the proportion of time spent resting or being vigilant was not.

Post hoc Tukey tests revealed that hares spent a greater mean proportion of time running during dawn and dusk compared to during the day or night (Fig. 3). Hares spent significantly less time feeding during the day compared to all other times of the day

(Fig. 3). Hares also spent significantly more time grooming during dawn and dusk times compared to during the day and night (Fig. 3).

Combining the behaviours into active and inactive behaviours and comparing between different parts of the day (dawn, day, dusk and night) showed that hares spent the majority of their time being inactive, this included resting and sitting/crouched behaviour (Fig. 4). Hares were more inactive during the day (one hour after sunrise to one hour before sunset) ($t = 16.123$, $df = 3$, $P = 0.001$) and the most active at night ($t = 5.963$, $df = 3$, $P = 0.009$).

Changes to daylight hours

Hares' behaviour significantly changed when daylight hours per day increased (Table 6). When daylight hours increased hares rested less and were more vigilant (Fig. 5), however the amount of time running, feeding or grooming did not change significantly. The only behaviour that was significantly different depending on time of day was running ($F = 9.595$, $df = 3,138$, $P = 0.001$); the other behaviours had no significant interaction between daylight hours and time of day. Hares increased the percentage of time they spent running at dawn, dusk and during the night when daylight hours reduced but decreased during the day (Fig. 6).

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Discussion

We were able to classify observed behaviours from the AcTag data with high accuracy (89 %) with only an 11 % error rate using the Random Forests method. This was similar to other studies that used Random Forests to classify behaviours from 3DA data (Rai *et al.*, 2012). Tri-axial accelerometers provide the technology to collect behavioural data on animals that otherwise could be hard to view (Shepard *et al.*, 2008; Nathan *et al.*, 2012; McClune *et al.*, 2014). However, validation of behaviours inferred from 3DA data has previously been extremely challenging. The individual accuracy of behaviours defined in our random forest model varied, with running (100 % accuracy), feeding (94.7 %) and vigilance (98.3 %) having the highest classification accuracy. However, there were some behaviours that the model failed to classify, such as hopping and licking that had 0 % classification accuracy.

Differences in classification class errors could be due to the number of examples of that behaviour that were filmed and, therefore, used to model the behaviour, similarities between different behaviours in the 3DA data that could cause error, or there was no clear pattern for those particular behaviours. Classification accuracy has been a common yet often unquantified problem in studies using 3DA technology, and is likely to vary between species. For example, McClune *et al.* (2014) found that walking, trotting and snuffling could not be distinguished from each other for a badger. Whereas, in our study crouching, vigilance and feeding could not be distinguished, as the head and hence the neck was moved whilst in a crouched position during all three behaviours. McClune *et al.* (2014) have suggested that optimising the size of the windows and increasing the number of parameters used could aid in increasing classification accuracy. By using windows to condense the data some of the information is lost. Gjoreski *et al.* (2010)

reported that micro activities, such as small movements or gestures, could be lost when condensing data to 5 second windows, which nevertheless accurately classified macro level activities such as walking. However, we found that summarising data into 5 second windows did reduce the amount of data noise and also reduced the computer power needed to analyse the data.

Our successful deployment of AcTags on hares, and robust classification of behaviours has allowed us to gain information on hare behaviour which compares with what little existing behavioural data exist from the wild. Our data was also able to compare behaviours and activity levels at different times of day, which was previously not possible using direct observational methods only. Hares spent the majority of their time being inactive, with the least activity during daylight hours, which was expected as they are crepuscular (Hutchings & Harris, 1996). When they were active they spent 46 % of the time being vigilant and 25 % feeding. The main behaviours that changed were feeding and vigilance, suggesting a possible trade-off between the two. There were increases in other active behaviours, such as running and grooming during the hours around dawn and dusk. At these times of day hares leave or return to their forms after resting or feeding (Monaghan & Metcalfe, 1985; Holley, 2001) and it is likely that they spend that time stretching or cleaning following resting or after a night's activity.

When daylight hours increased there was a significant reduction in time spent resting and feeding and an increase in vigilance. It is possible that the increase in daylight hours affects hares' perception of predation risk or is associated with higher levels of disturbance. Holley (2001) also found that as daylight hours increased hares were more active during daylight hours but could not relate this to reproduction or feeding

requirements. In that study hares were active for at least 12 hours, irrespective of number of daylight hours per day (Holley, 2001), so must have been active during daylight hours in the summer months when night time reduced below 12 hours.

The only behaviours that were affected by the change in daylight hours and the time of day were running and vigilance, which increased at dawn, dusk and night but reduced during the day. This is consistent with the time around dawn and dusk being spent moving between sites, or perhaps interacting with other hares, and being more cautious, as daylight hours increased. This latter observation is also consistent with observations of Monaghan & Metcalfe (1985) that group vigilance did not alter due to light intensity at dawn and dusk. However, in the current study hares did not increase feeding at dawn and dusk, as most feeding activity was carried out at night. Holley (2001) suggested that daylight is an inhibitory factor to hares activity, and that hares are less daylight-shy when they are hungry, and hence search for food. In this study the difference in day length was only 2 hours, but nevertheless was associated with significant changes to behaviour. Data collected over a longer time period may have demonstrated greater behavioural differences with greater differences in daylight hours.

Due to the small sample size we cannot identify possible differences between individual hares, male or female behaviour or seasonal variability. This would require further development of the tag analysis methods and remote data collection to cope with larger sample sizes, as well as, a reduction in costs of the AcTags to deploy large numbers of tags.

The benefit of using AcTags was that they provided a continuous log of activity that revealed patterns in hare behaviour that would not otherwise have been recorded. This suggests there could be potential biases in our understanding of hare behaviour from direct observation studies that have primarily been carried out at dawn or dusk. Linking 3DA data with location data could provide detailed insight into the interplay of behaviour and habitat use (Bruno *et al.*, 2015). Future developments in tracking technology may permit AcTags with GPS units which are light enough to be deployed on hares and other small mammals and would provide concurrent spatial data to assess habitat-specific behaviour. However, the processing and analysis of the vast amounts of data collected by AcTags, and other 3DA based tags, require significant time and computer processing power. Standardisation of data management and analysis tools would facilitate comparisons between studies, and may allow retrospective re-analysis of previous studies for comparative purposes.

Conclusion

Our AcTags enabled us to collect behavioural data on hares for an unprecedented length of time both day and night that has not been done previously. The Random Forest method was highly accurate at classifying behaviours from supervised models using known behaviours. It is clear that this technology could be used to answer many ecological questions, but methods used to analyse the 3DA data need to be developed to make the process quicker, simpler and more accurate. AcTags offer huge possibilities for the study of mammal behaviour, as they are able to collect data when observations are difficult in the wild and over much longer periods. This will help further our knowledge of animal ecology and behaviour immensely and consequently better inform management policies and conservation.

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Tables

Table 1: Classification of behaviours of hares

Behaviour	Description
Vigilant	Either sitting up or in a crouched position, head is raised.
Feeding	Crouched position with head down, biting or chewing, moving head side to side.
Running	Larger movements involving greater distances either within fields, to a new area, or moving into different fields
Hopping	Smaller movements within the same patch, of a few hops usually during feeding
Grooming	Scratching, licking parts of the body or stretching
Resting	Crouched lower to the ground, relaxed rather than alert
Interaction	Chasing another hare/rabbit or being chased

Table 2: Mean 3-Dimensional acceleration data for x, y and z axis recorded of the nine identified behaviours

Behaviours	Mean acceleration ($m\ s^{-2}$) x axis	Mean SD x axis	Mean acceleration ($m\ s^{-2}$) y axis	Mean SD y axis	Mean acceleration ($m\ s^{-2}$) z axis	Mean SD z axis
Resting	10.29	1.85	-17.50	2.39	-21.74	1.26
Running	9.78	7.86	-32.45	12.47	5.55	4.32
Vigilance	11.12	0.82	-23.60	2.86	-14.37	3.69
Feeding	8.58	1.56	-29.47	0.91	6.64	4.27
Scratching	5.64	0.66	-22.52	9.07	-10.87	9.05
Licking	9.36	0.26	-26.02	6.82	-1.90	6.38
Shaking	4.77	0.56	-20.90	8.42	-16.04	3.78
Hopping	14.93	3.57	-25.26	1.50	0.22	3.25
Stretching	11.17	2.46	-24.00	1.57	8.00	3.21

Table 3: Summary of 3-Dimensional Acceleration data collected from each tagged hare

Hare ID	Number of days of data	Number of 3DA data points
3530 (Female)	34	144 413 696
3531 (Male)	33	145 070 848
3532 (Female)	0	Tag failed
3533 (Female)	33	144 651 264
3534 (Female)	12	60 688 256 (Died half way through)

Table 4: Confusion matrix of the classification of behaviours from the training data. Predicted behaviours are the rows and actual behaviours are the columns. The class error indicates how well the behaviour has been classified with 0 representing definite positive classification and 1 being poor classification. Those shaded grey have been classified very well.

	Rest	Run	Vigilance	Feed	Scratch	Lick	Shake	Hop	Stretch	Class error	Accuracy %
Resting	7	0	5	2	0	0	0	0	0	0.50	50
Running	0	8	0	0	0	0	0	0	0	0.00	100
Vigilance	0	0	162	8	0	0	1	0	0	0.05	94.7
Feeding	0	0	3	178	0	0	0	0	0	0.02	98.3
Scratching	1	0	2	1	3	0	2	0	0	0.67	33.33
Licking	0	0	1	2	0	0	0	0	0	1.00	0
Shaking	0	0	0	1	4	0	1	0	0	0.83	0
Hopping	0	0	2	5	0	0	1	0	0	1.00	0
Stretching	0	0	1	0	0	0	0	0	0	1.00	0

Table 5: Analysis of behaviours at different times of the day.

Results of ANOVA using logit-transformed mean proportion of time hare behaviours (resting, running, vigilance, feeding and grooming) were carried out at different times of the day (dawn, day, dusk and night). Values in bold are significant.

	F	**df**	**P**
Time of day			
Resting	1.091	3, 138	0.352
Running	**21.126**	**3, 138**	**0.001**
Vigilance	1.470	3, 138	0.222
Feeding	**10.068**	**3, 138**	**0.001**
Grooming	**10.995**	**3, 138**	**0.001**

Table 6: Analysis of behaviours when day length increases.

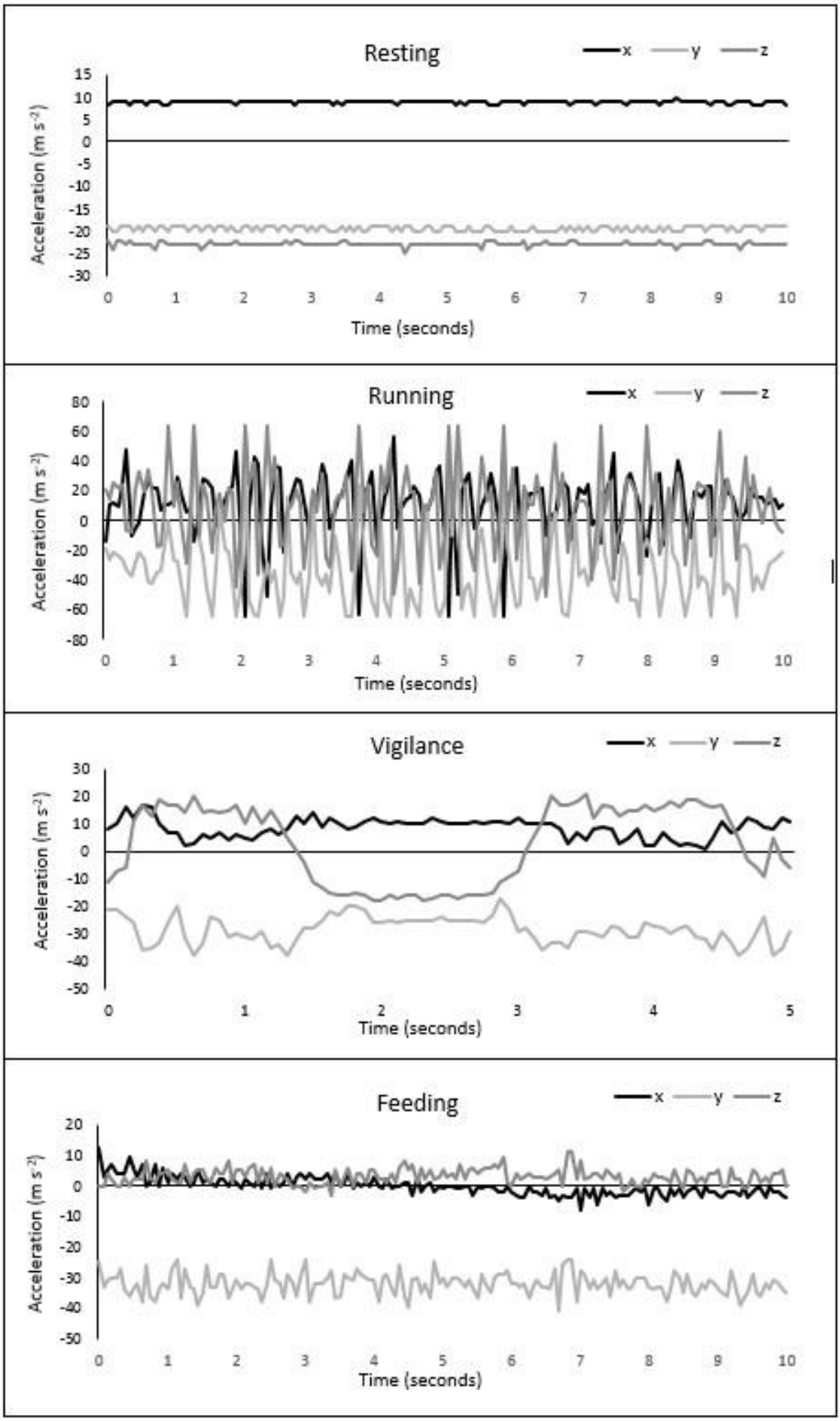
Results of ANOVA using logit-transformed mean proportion of time hares carried out behaviours (resting, running, vigilance, feeding and grooming) between different number of daylight hours per day. Significant values are in bold.

	F	**df**	**P**
Daylight hours			
Resting	**16.652**	**1, 140**	**0.001**
Running	0.720	1, 140	0.401
Vigilance	**13.294**	**1, 140**	**0.001**
Feeding	0.884	1, 140	0.349
Grooming	1.315	1, 140	0.254

Figures

Figure 1: Accelerometer data of four hare behaviours

3-dimensional acceleration data (x, y, z axis) recorded on the tri-axial accelerometer tags as examples of the patterns identified of known behaviours that were recorded from filming the tagged hares.


Resting
x
y
z
Acceleration (m s-2)
15
10
5
0
-5
-10
-15
-20
-25
-30
0
1
2
3
4
5
6
7
8
9
10
Time (seconds)
Running
x
y
z
Acceleration (m s-2)
80
60
40
20
0
-20
-40
-60
-80
0
1
2
3
4
5
6
7
8
9
10
Time (seconds)
Vigilance
x
y
z
Acceleration (m s-2)
30
20
10
0
-10
-20
-30
-40
-50
0
1
2
3
4
5
Time (seconds)
Feeding
x
y
z
Acceleration (m s-2)
20
10
0
-10
-20
-30
-40
-50
0
1
2
3
4
5
6
7
8
9
10
Time (seconds)

569

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571 **Figure 2: Variable importance graph**

572 Variable importance graph of the Random Forest classification model on the 75 % of

573 the data used for model training.

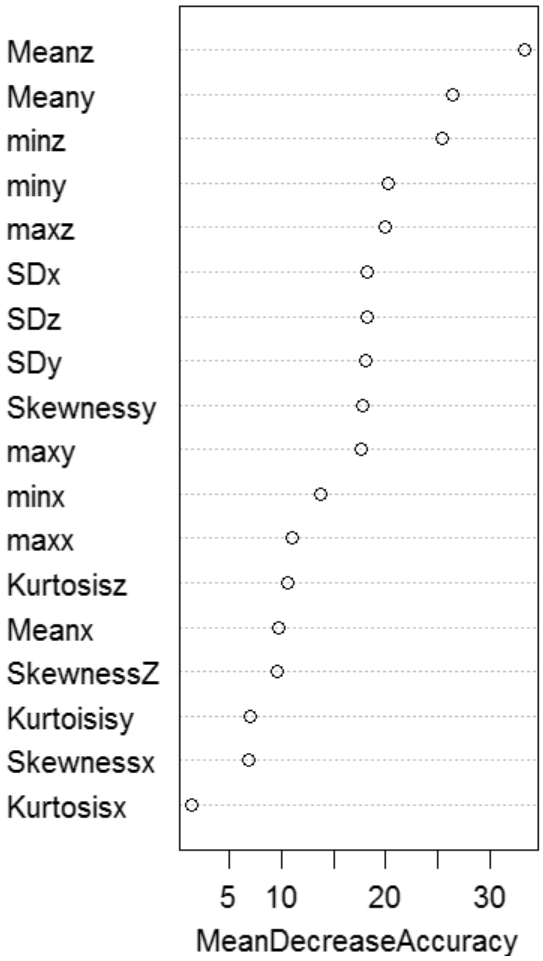

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Figure 3: Hare behaviour at different times of the day

Mean percentage of time hares spent doing behaviours during different times of the day. Error bars are standard deviation.

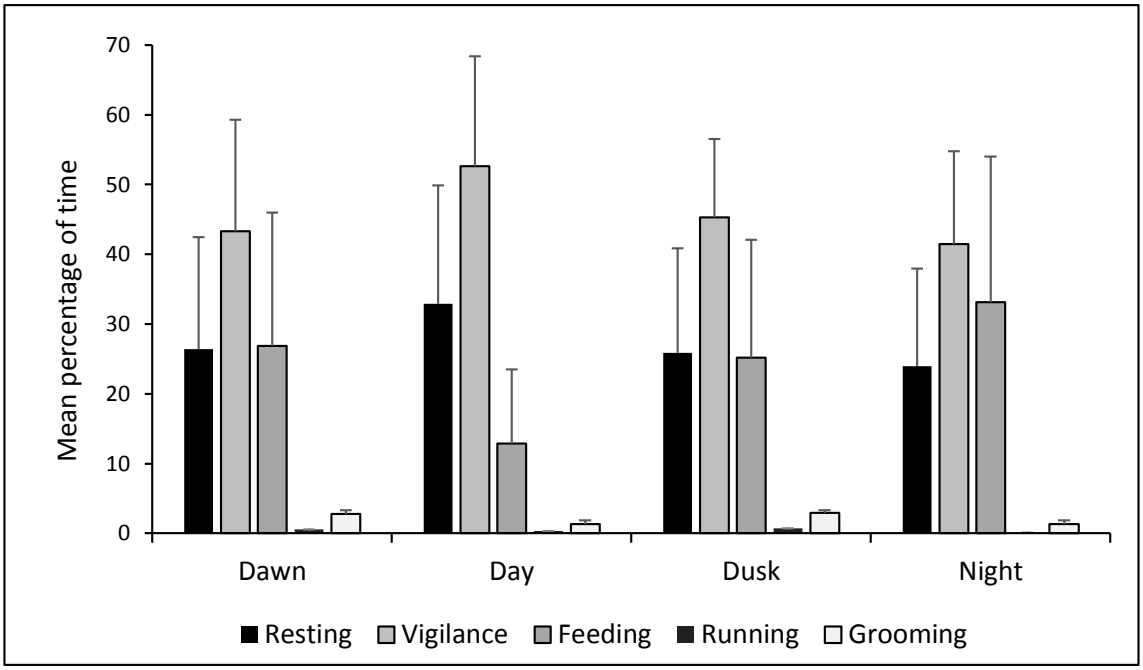
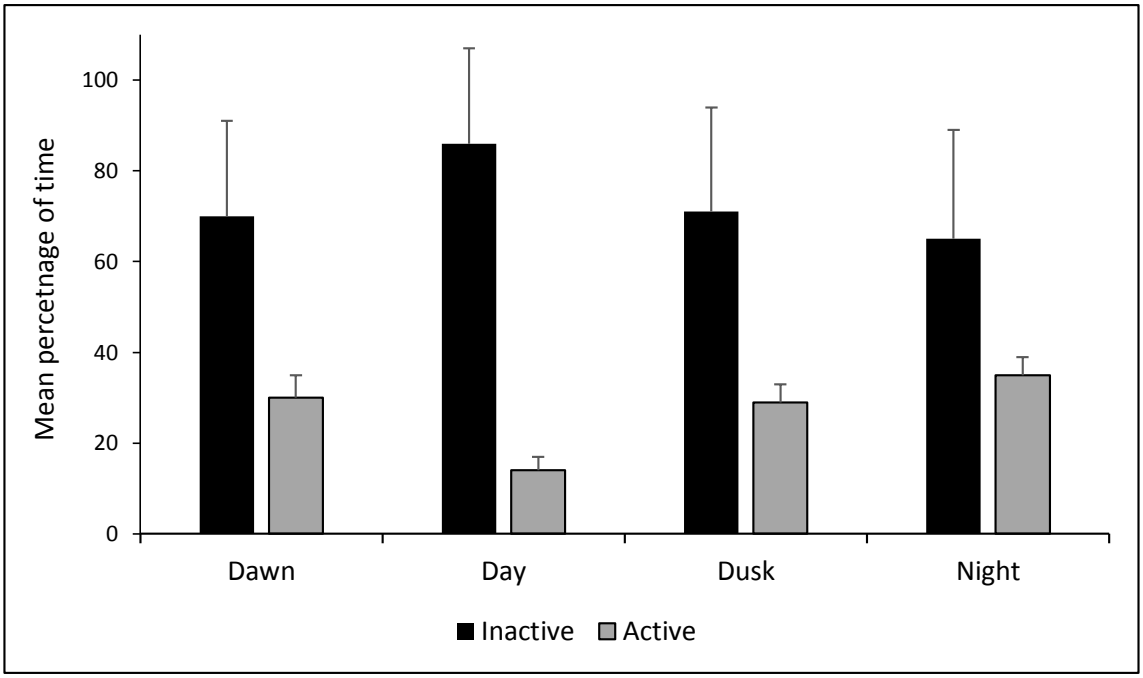


Figure 4: Hare activity at different times of the day

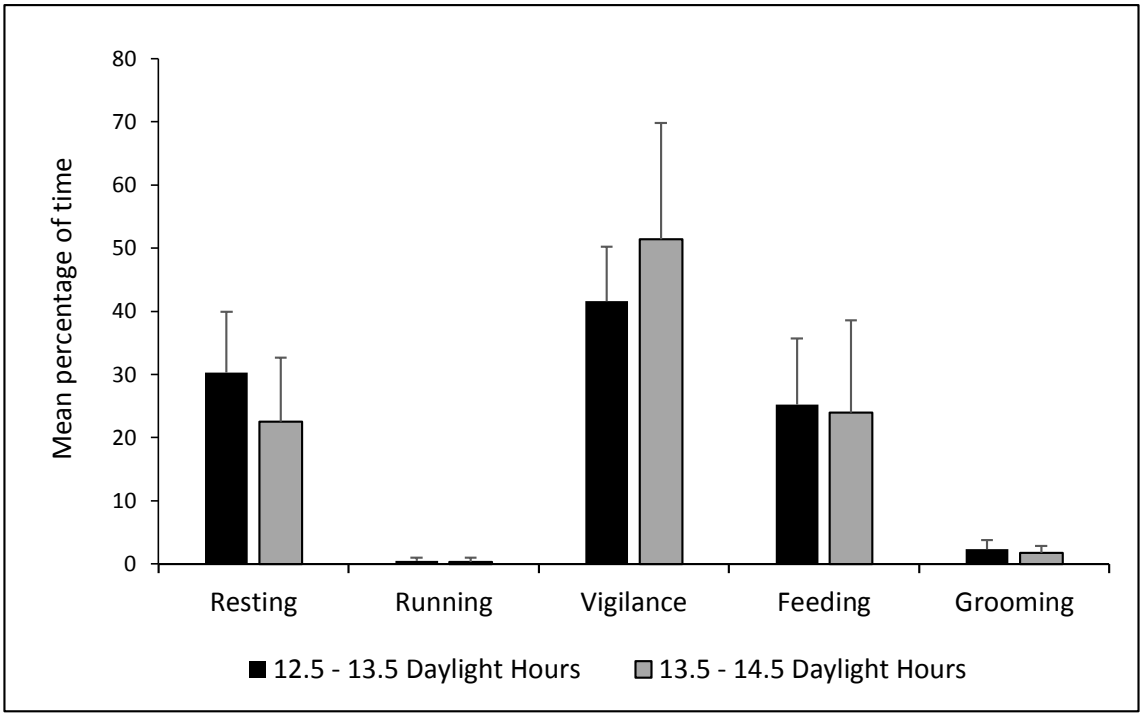
Mean percentage of time hares spent active and inactive during different times of the day. Error bars are standard deviation.



588 **Figure 5: Hare behaviour when daylight length increases.**

589 Mean percentage of time hares spent doing behaviours between different number of

590 daylight hours. Error bars are standard deviation.



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592

Figure 6: Hare running behaviour at different times of day and day length

Mean percentage of time hares spent running at different times of the day and between different amounts of daylight hours. Error bars are standard deviation.